

REPRODUCTIVE BIOLOGY OF CANYON WRENS IN THE FRONT RANGE OF COLORADO

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ABSTRACT.—Canyon Wrens (*Catherpes mexicanus*) occur throughout the semiarid regions of the western United States in habitats dominated by canyons and steep rock formations. Their inaccessible habitat has made them one of the least studied among North American birds. We studied a population of Canyon Wrens in the Front Range of Colorado, documenting many aspects of their breeding biology. We report on territory density and size, nest site characteristics, nesting phenology, nesting success, and nestling development. Received 3 May 2002, accepted 15 November 2002.

Canyon Wrens (*Catherpes mexicanus*) are found locally in semiarid regions of the western United States in habitats dominated by rocky substrates such as canyons, escarpments, and other areas with precipitous formations (Jones and Dieni 1995). Inaccessibility of their habitat has made Canyon Wrens one of the least studied among North American birds (Jones and Dieni 1995, Johnston 1998). Consequently, we undertook a study to obtain baseline information on this species in an effort to learn more about its reproductive natural history. In this paper, we present observations of a Canyon Wren population in central Colorado, including territory density and size, nest site characteristics, nesting phenology, nesting success, and nestling development.

METHODS

Our primary study site was located at Red Rocks Amphitheater and Mountain Park, situated in the Front Range uplift zone of the Rocky Mountains, 20 km southwest of Denver, Colorado (39° 40' N, 105° 12' W; elevation 1,890 m). This site encompassed 1,093 ha, including 280 ha of rock outcrops ≤140 m in height. Exposed substrates are dominated by red, arkosic sandstone and conglomerate rock outcrops of the Pennsylvanian Fountain formation, flanked by Precambrian metamorphic gneiss and schist of the Idaho Springs formation, with Lyons formation sandstone at the base (Taylor 1999). The climate is continental and semiarid; mean annual precipitation is approximately 41 cm for the region. Daily high and low temperatures were a

mean of 7 and –8° C, respectively, for January, and 30 and 14° C, respectively, for July (1962–2000, Lakewood weather station; data from Western Regional Climate Center, Desert Research Inst.). We also obtained reproductive data from a second site located near Evergreen, in the interior foothill region of the Front Range (39° 38' N, 105° 21' W; elevation 2,380 m).

We conducted breeding surveys from April to September during 1994, 1996, and 1999–2001 and winter surveys from November 1999 to February 2002. We surveyed suitable habitat at Red Rocks Park weekly using tape playback broadcasts of Canyon Wren songs and calls. Once sighted, an individual bird was followed visually and its locations mapped. We determined territory size by plotting boundaries from a mean of 23 (range = 6–68) locations during breeding surveys and a mean of 10 (range = 4–25) locations during winter surveys. We calculated density as the number of territories per 100 ha of rock cover.

We conducted nest searches during the breeding seasons of 1999–2001 using observation and behavioral cues (Martin and Geupel 1993). Once located, nests were monitored every 2–4 days to completion; we documented nesting phenology, clutch size, and number of young fledged. For behavioral observations, we identified the sex of the adults by behavior. Sex was presumed only when both members of the pair were visible and sex was apparent by behavior (e.g., male song).

Nest measurements included nest height (from ground to center of nest), nest rock height, nest site type (e.g., cavity, crevice), nest site slope, and nest and nest site orientation. We used Rayleigh's test (Zar 1999) to test for circular uniformity in orientation of nest and nest site entrance ($P < 0.05$). Several nests were inaccessible and this is reflected in the different sample sizes reported for individual measurements. Measurements for inaccessible nest rocks and nest entrances were estimated where possible using a clinometer and range finder.

RESULTS AND DISCUSSION

Territory density and size.—Summer territory density at Red Rocks Park was con-

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TABLE 1. Characteristics of nest sites and rocky nest substrate for Canyon Wrens in the Front Range of Colorado, 1999–2001.

Statistic	Height of nest (m)	Height of nest rock (m)	Nest height/rock height ratio	Circumference of entrance (cm)	Entrance area (cm ²)	Cavity volume (cm ³)
Mean	6.7	13.5	0.49	55.5	435	1200
Range	0.8–18.4	1.4–40.4	0.06–0.88	24.4–51.6	47–3200	63–5100
<i>n</i>	16	16	16	10	10	10

sistent among years, with a mean of 4.5 per 100 ha (SD = 0.5, $n = 4$ years). Summer territory size was more variable, ranging from 0.4–2.8 ha across all years (mean = 1.3 ha \pm 0.6 SD, $n = 5$ years). Winter densities were lower (3.4 per 100 ha \pm 0.3 SD, $n = 3$ years), and territories were smaller, ranging from 0.2–1.9 ha across all years (mean = 1.0 ha \pm 0.4 SD, $n = 4$ years). The smaller mean winter territory size could be a result of their lower responsiveness to tape playback during the winter.

Comparing our estimates of territory size and the total area of rock cover at Red Rocks Park suggests that apparently suitable habitat was not being occupied every year. Territory size likely was underestimated, although this alone cannot account for the discrepancy. One hypothesis is that winter survival may be limiting population size. We observed a 17% decline in summer territory density at Red Rocks Park between the breeding seasons of 2000 and 2001. Areas used for territories in some years were not always occupied during successive years; we observed a mean occupation rate of 57% ($n = 14$) across years ($n = 5$).

Nest sites.—Nests ($n = 28$) always were placed in rocky substrates, predominantly the large outcrops from the Fountain formation, but they also were placed in the smaller rocks and boulders occurring at the base of these outcrops. The use of smaller-sized rocks (<2 m²) as nest sites (25%, $n = 7$), was in agreement with the findings of Johnston (1998) in southern Idaho. Nests ($n = 21$) were placed in an enclosed, protected space, which included 12 (57%) in rock cavities, 6 (29%) in crevices, 2 (10%) in tubes, and one (5%) on a ledge inside a cave. Of these nest sites, 12 (57%) were on vertical rock faces, 3 (14%) on sloping rock <50°, 5 (24%) in groups of smaller rocks, and one (5%) on an isolated

small rock. Three nests (14%) also occurred in caves or in multiple rocks that formed a cave-like structure, and six (29%) had protective rock overhang that extended 2–18 cm above the nest site.

There was no apparent pattern of nest placement with respect to available rock height, suggesting that microsite characteristics alone determined nest site selection (Table 1). Nest sites had a mean southern orientation of 158° ($z = 3.48$, $P = 0.028$). In contrast, nest entrance orientation did not differ significantly from what would be expected by chance from a uniform distribution ($z = 0.21$, $P = 0.81$). Southern orientation of nest sites undoubtedly confers thermal benefits with direct exposure to solar rays during the spring months. However, enclosed nest sites such as rock cavities and crevices may moderate hot outside air temperatures that occur during the summer months. Nest site microhabitats were found to be cooler than outside temperatures during the summer months in Idaho (Johnston 1998). In our study, all nests were protected from direct sunlight and were sheltered from wind and rain.

Nest characteristics.—During 1999–2001, we located and monitored 20 nests at Red Rocks Park. We also report data from an additional eight nests that we opportunistically located between 1993 and 2000. Two (7%) of the nests ($n = 28$) were reused during the same year, five (18%) in subsequent years, and two (7%) during three consecutive years. Eight (29%) of the pairs had second broods during the same year, and one successfully fledged a third brood. We observed six nests (21%) being torn down by an adult after the young fledged, and the contents were scattered below the nest site.

All nests contained a twig base, interconnected with various plant fragments, including dead leaves and seeds. This base served as

TABLE 2. Reproductive data for Canyon Wrens in the Front Range of Colorado, 1999–2001.

Statistic	Clutch size	Brood size	Number of fledglings per successful nest	Number of fledglings per nest	Incubation period (days)	Nestling period (days)	Total nesting period (days)
Mean	4.5	3.9	3.6	2.9	16.9	16.9	37.5
SD	0.9	0.8	1.0	1.3	1.4	1.7	3.2
Range	2–6	2–6	2–6	2–6	13–19	12–19	29–41
<i>n</i>	22	21	23	28	17	17	15

foundation for a soft cup nest, which contained moss, feathers, and animal hair. In addition, we also observed artificial fragments such as paper, plastic, lint, yarn, and even a rubber band. Mean weight of the soft cup ($n = 4$) was 26.5 g.

Nesting phenology and nesting success.—Clutches ($n = 23$) were initiated between 23 April and 15 August, 1994–2001, although breeding has been documented as early as 20 March in Colorado (Jones 1998). Median clutch initiation date was 17 May, with the peak on 15 May (range = 23 April to 26 June). Reproductive data are presented in Table 2.

Of the nests we monitored ($n = 28$), 22 (79%) successfully fledged young, 2 (7%) had unconfirmed outcomes but were thought to be successful since we observed fledglings in the area, and 4 (14%) failed. Of the nests that failed, two were depredated, one was destroyed by climbers, and one failed due to weather. Renesting occurred ≤ 7 days following failure for all failed nests. We found two nests that had only the twig bases constructed and were not used further, suggesting that they might be surplus (“dummy”) nests similar to the unused nests constructed by other species of the family Troglodytidae (Brewer 2001). This behavior has not been documented previously for Canyon Wrens.

Nestling development.—We documented the development of nestlings at two nests. After hatching, nestlings were altricial, pink, weak, with their eyes closed (Appendix). Near the nests, females used a previously undocumented call (Jones and Dieni 1995) that resembled a rolling buzz, a deep *grrrrr*. The female increased her use of this call as the nestlings neared fledging. We observed fledging at three nests. On all three occasions, fledging began within the first 2 h of dawn. It took ≤ 2 h for all young to leave the nest

for the first flight, and throughout the morning they returned to the nest frequently. They returned to the nest site at night to roost for ≤ 2 days after fledging. Once fledged, they remained under parental care ≤ 21 days. During this period fledglings continued to call, using high pitched *cheeps* that resembled the adult alarm call. We observed the male care for the fledglings early in the breeding season, while the female established another nest. The male and fledglings gave alarm calls continuously.

Our data provide much needed information on the basic aspects of Canyon Wren breeding biology. However, since these data may not be representative of all Canyon Wren populations, replication of this study is warranted for other populations throughout this species' range. It would be of interest to make comparisons between populations in the northern extremes and the southern interior to determine how nest site habitat relationships and nesting phenology vary according to parent substrate, land form, and climate.

ACKNOWLEDGMENTS

We thank M. Dirks, S. Fellows, A. Kantola, R. Kluever, and R. Robinson for their assistance in the field. We also thank D. Klute for analyzing the nest orientation data, for assisting in the field, and for reviewing earlier versions of this manuscript. G. Geupel, J. Hansen, R. Hansen, H. Johnston, and G. Miller provided helpful suggestions, observations, and insights. We are grateful to J. Mola for allowing us access to his property, and to J. E. Cornely for providing resources and other support during the course of this study. In addition, we thank two anonymous reviewers for their helpful suggestions and improvements to this manuscript.

LITERATURE CITED

- BREWER, D. 2001. Wrens, dippers, and thrashers. Yale Univ. Press, New Haven, Connecticut.
JOHNSTON, H. L. 1998. Canyon Wren ecology, Lower

- Salmon River Gorge, Idaho. M.Sc. thesis, Univ. of Idaho, Boise.
- JONES, S. L. 1998. Canyon Wren. Pp. 460–461 in Colorado breeding bird atlas (H. E. Kingery, Ed.). Colorado Bird Atlas Partnership and Colorado Div. of Wildlife, Denver.
- JONES, S. L. AND J. S. DIENI. 1995. Canyon Wren (*Catherpes mexicanus*). No. 197 in Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.
- MARTIN, T. E. AND G. R. GEUPEL. 1993. Nest monitoring plots: methods for locating nests and monitoring success. *J. Field Ornithol.* 64:507–519.
- TAYLOR, A. M. 1999. Guide to the geology of Colorado. Cataract Lode Mining Corp., Golden, Colorado.
- ZAR, J. H. 1999. Biostatistical analysis, 2nd ed. Prentice Hall, Upper Saddle River, New Jersey.

APPENDIX. Canyon Wren nestling development, $n = 2$ nests and 6 nestlings, from Red Rocks Park, Morrison, Colorado, June and July, 2000.

Day	Characteristics
Days 1–2	At hatching, head bent down, legs stretched forward, nestlings resting largely on belly, which is conspicuously distended and remains so for the first few days. Skin grey-pink; eyes closed, grey to blackish-grey; bill and feet pink; egg tooth light yellow-white; mouth lining bright yellow; down grey, in sparse tufts on crown. No feather tracts. Weight: 2.15 g.
Day 3	Eyes closed, grey. Feather tracts: dorsal and alar raised black dots, ventral faint yellow dots; capital and caudal not evident. Weight: 3.30 g.
Day 4	Egg tooth gone. Feather tracts: dorsal raised black dots; alar pin feathers faint, 0.5 mm; ventral faint yellow dots; caudal not evident; capital with grey down. Weight: 6.90 g. Gape: 9.34 mm; culmen: 6.45 mm; tarsus: 10.10 mm; total length: 37.68 mm.
Days 6–7	Skin pink to dark pink; eyes open, blue-black; mouth lining light yellow to orange. Feather tracts: dorsal pin feathers 1.75 mm, longest primary sheath 3.93 mm, greater coverts 5.07 mm; ventral light-grey dots raised 0.1 mm; caudal barely visible, slightly raised. Weight: 7.70 g. Gape: 10.19 mm; wing chord: 15.51 mm; tarsus: 13.99 mm, total length: 47.14 mm.
Day 9	Faint calls. Skin pink; grey down on head and back. Feather tracts: dorsal, alar, and capital broken. Dorsal: feather 1.31 mm, sheath 3.50 mm; longest broken primary (LBP) feather 0.5 mm, sheath 11.03 mm. Sheaths: capital: 2.74 mm; greater coverts: 3.57 mm; ventral: 2.87 mm; caudal: 3.86 mm. Weight: 7.80 g. Gape: 11.17 mm; wing chord: 21.28 mm; tarsus: 19.19 mm; total length: 47.55 mm.
Day 10	Chipping calls. Eyes black. Weight: 9.20 g. Gape: 12.76 mm; culmen: 7.77 mm; tarsus: 20.88 mm; wing chord: 27.00 mm; 6th rectrix: 8.05 mm; total length: 54.30 mm.
Days 11–12	Loud, high pitched begging calls, crouching, movement away from observer. Bill and feet grey-pink; mouth lining light yellow to orange. All feather tracts broken. Weight: 12.00 g. Wing chord: 37.76 mm; tarsus: 20.6 mm; 6th rectrix: 13.84 mm; total length: 51.91 mm.
Days 14–15	Skin dark grey-pink; eyes all open, iris dark brown; bill and feet pinkish-brown; mouth lining light yellow; gape bright yellow. All feather tracts complete. Fat high. Weight: 12.50 g. Culmen: 7.31 mm; wing chord: 38.17 mm; tarsus: 22.2 mm; LBP: 14.60 mm; rectrices: 15.48 mm; 6th rectrix: 13.98 mm; total length: 61.75 mm.
Day 17	Day before fledging. Skin pink; eyes black; mouth lining yellow-orange. All feather tracts complete and all with sheathing, plumage pattern adult-like, but looser, with down and more white spotting on breast. Weight: 11.23 g. Culmen: 9.39 mm; wing chord: 40.15 mm; 3rd primary, feather: 24.52 mm, sheath: 14.79 mm, LBP: 16.29 mm; tarsus: 23.81 mm; 6th rectrix 15.20 mm, sheath 6.68 mm, total length 63.21 mm.